SOME DEMOGRAPHIC AND ALLOMETRIC CHARACTERISTICS OF *ACACIA SMALLII* (MIMOSACEAE) IN SUCCESSIONAL COMMUNITIES

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ABSTRACT

Diameter distributions of *Acacia smallii* Isley were examined in the South Texas Plains Region in a series of successional communities ranging in age from 15 yr to mature stands >150 yr. In the 15 yr stand, all individuals were in the sapling stage and the size class distribution was non-normal and positively skewed. Mid-successional and older woodland communities had distributions that approached normal curves. Mean live basal area of *A. smallii* increased in stands up to 25–29 yr, and then declined. There was no recruitment of *A. smallii* in stands 19 yr or older. The mean number of stems per plant increased and then decreased in the progression from younger to older stands. Dead stems increased from zero in the 15 yr stand to 66% of the *A. smallii* density in the 33 yr stands. Of the total *A. smallii* basal area, ca. 70% was dead tissue in the 33 yr stands. No individuals of *A. smallii* were present in the mature forest community. Possible cause of this lack of *A. smallii* recruitment was the low light environment caused by canopy closure. Demographic analyses of *A. smallii* diameter distributions suggest it is an early successional species.

Acacia smallii Isley (huisache) is found throughout the southern United States from northern Florida to California (Correll and Johnston 1970). In south Texas, it is reported on approximately 1.1 million ha with more than 20% cover occurring in some places (Smith and Rechenthin 1964). *Acacia smallii* is a heliophyte (Bush and Van Auken 1986a), and is tolerant of low levels of soil nitrogen (Van Auken et al. 1985). *Acacia smallii* has been reported as an early successional species in south Texas (Van Auken and Bush 1985); however, there are no reports of demographic or allometric characteristics of this species.

Studies of demographic characteristics of long-lived woody plants in natural plant populations are scarce (Harper 1977). Whittaker (1975) suggested that early successional species, those that would not remain in a mature forest community, developed normal distributions, whereas the mature forest species had negative exponential distributions. Mohler et al. (1978) proposed idealized frequency distributions of trunk diameters for selected stages in succession. During stand establishment, the frequency distribution is a negatively skewed function. After establishment, but before the start of thinning, the distribution approaches a normal curve; at the start of
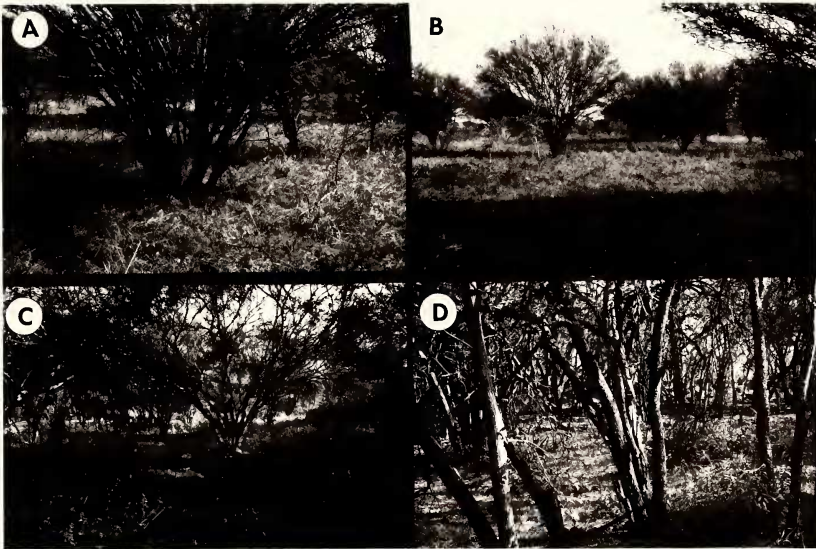
FIG. 1.   Habitats of *Acacia smallii* during several stages of secondary succession.
A. Multi-stemmed growth form of *A. smallii*. B. Early open savanna or woodland
stage with a high grass density in the understory. C. Canopy closure during the late
savanna stage. D. Early mature forest stage with most *A. smallii* dead, and the presence
of other deciduous species in the overstory.

thinning the distribution is positively skewed. Finally, during late
thinning the curve again approaches a normal distribution. Other
studies, although less comprehensive, showed that disturbance se-
quence, site or niche difference, and initial density or spacing were
all factors that had a role in determining the demographics of a
species (Koyama and Kira 1956, Davidson and Donald 1958, Yoda
et al. 1963, Leak 1975, Crisp and Lange 1976, Crisp 1978, Harcombe
and Marks 1978, Ross et al. 1982, Knowles and Grant 1983, West
and Borough 1983).

In addition to changes in the demographics of a plant population,
increased competition causes alterations in the morphology of in-
dividual plants (Harper 1977). Morphological changes occur in whole
plants, for example, as shown in the annual diameter growth of *Picea
sitchensis* (Bong.) Carr. at various spacings (Jack 1971). Additional
changes in whole plant morphology were demonstrated in *Pseudo-
tsuga menziesii* (Mirb.) Franco, which showed a larger number of
suppressed individuals at higher densities (Curtis and Reukema 1970).
Jack (1971) demonstrated a reduction in the number of branches in
Picea sitchensis grown at high densities.

The purposes of this study were to examine some demographics
of population development and decline of *Acacia smallii,* and to
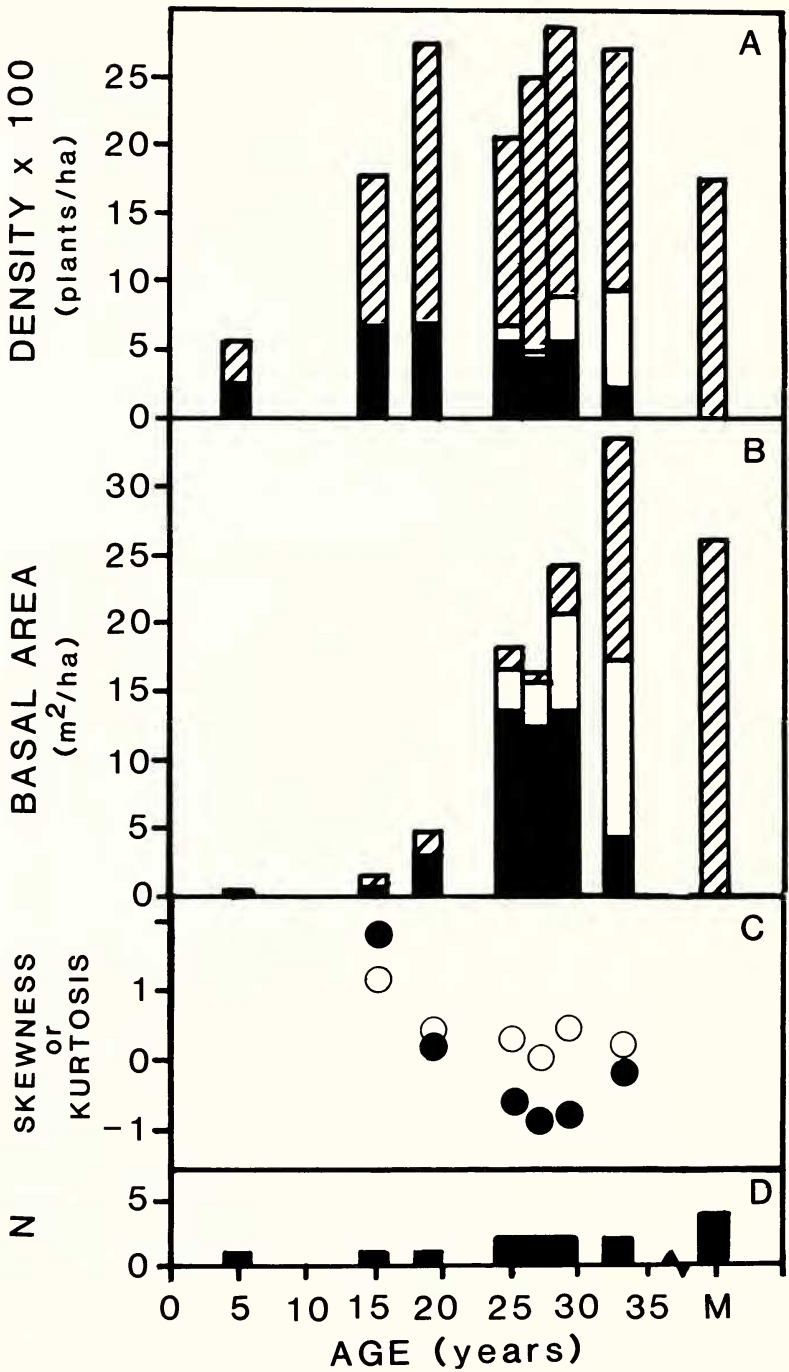
examine some allometric changes of this species associated with temporal change.

METHODS

This study was conducted in the northern portion of the South Texas Plains Region of Texas (Gould 1969). Fifteen communities in various stages of secondary succession were selected for detailed analyses. The sites were located on flood plain terraces of the San Antonio River, which potentially support riparian woodland or forest communities (for locations see Van Auken 1982, Bush and Van Auken 1984). Climate of the upper San Antonio River area is dry subhumid (Thornthwaite 1948). This area receives approximately 71 cm/yr rainfall, with a mean annual temperature of 15.5°C (Carr 1967, Arbingast et al. 1976). Soils are deep loams (240–310 cm), that usually are well drained, calcareous, and friable (Taylor et al. 1966, Taylor 1977).

Candidate stands were examined during a series of field surveys. Stands also were located on aerial photographs and soil survey maps, and local residents were interviewed concerning past history of the sites. Selection was based on stand area, lack of additional disturbance other than light grazing in the mature communities, uniformity of physical features, and vegetation. Selected stands depicted various stages in a chronological sequence from open fields to mature forests.

The stands selected for study were 1–5 ha in size, and the area sampled in each stand ranged from 0.1–0.5 ha. Most of the stands were cleared in the 1950's. The mature stands were estimated to be in excess of 150 yr, as based on tree ring analyses.

Stands were sampled using belt transects, with 5 m × 5 m quadrats (Greig-Smith 1983). Density and basal area for all species except *A. smallii* were pooled. All stems greater than 1.0 cm in diameter at breast height were used to construct diameter distribution plots.

Demographic characteristics for the various stands were analyzed by size class (diameter). The width of the size classes in each stand was determined by dividing the range of diameters into 12 equal size classes (Mohler et al. 1978). Statistical tests included Chi-square analysis to test for normal distributions and a "t" statistic to test for skewness (g_1, asymmetry) and kurtosis (g_2, peakedness) (Sokal

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FIG. 2.   Live (■) and dead (□) standing stem density (A) and basal area (B) for *Acacia smallii* and all other woody species combined (▨) for a series of successional stands. Asymmetry (skewness = ○) and peakedness (kurtosis = ●) of the *A. smallii* populations also are presented (C) with the number (N) of stands sampled (D). M = mature stands greater than 150 yr old.
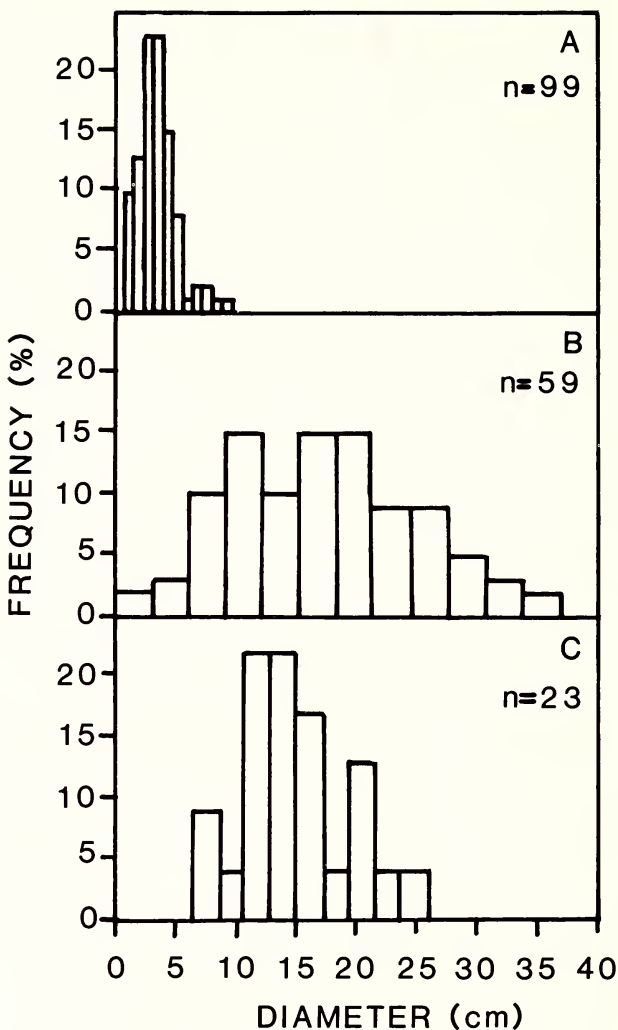
FIG. 3. Frequency distribution of live stems of *Acacia smallii* in secondary succession including a 15 yr stand (A), a 27 yr stand (B), and a 33 yr stand (C). n = the total number of plants measured in each stand, the distributions are not normal (Chi-squared, p ≤ 0.05).

and Rohlf 1981). An example of a 15, 27, and 33 yr stand is presented. Several morphological characteristics of *A. smallii* were examined including the number of stems per plant and the number and percent of dead stems per plant for each stand.

For determination of stand age, 52 plants of *A. smallii* (of various sizes and from various stands) were cored using the increment coring

technique (Fritts 1976). Regression analysis (Steel and Torrie 1980) was performed between tree diameter and tree age using all 52 samples ($r = 0.88$, $p \leq 0.001$). Next, the diameters of the five largest trees in each stand were used to estimate the stand age. Stand age was determined by adding 5 yr to the mean tree age (from regression) to account for seed recruitment and an additional 3 yr to account for growth from ground level to breast height (measured differences).

Results

Some typical flood plain terrace habitats that include *A. smallii* are shown in Fig. 1. Secondary succession begins with a community disturbance. Within 5 yr, *A. smallii* and other woody species colonize the area (Fig. 2A). *Acacia smallii* increased in density and basal area for the next 25 yr and dominated the stands (Fig. 2A,B). Dead *A. smallii* first appeared in 25 yr stands. Of the total standing basal area in 25 yr stands, ca. 16% was dead *A. smallii*. This value increased to ca. 39% of the total standing basal area in the 33 yr stand. In the 33 yr stand, 74% of the *A. smallii* basal area was dead tissue. *Acacia smallii* density followed a similar trend. Species composition shifted and stands greater than 30 yr had a high density and basal area of *Celtis laevigata* Willd. *Acacia smallii* was not present in the mature stands, which were dominated by *C. laevigata, Carya illinoinensis* (Wang.) K. Koch. and *Ulmus crassifolia* Nutt. (see Bush and Van Auken 1984, Van Auken and Bush 1985).

None of the stands examined had statistically normal distributions for *A. smallii* (Chi-square analyses $p \leq 0.05$). Skewness decreased from the highest value (1.08) in the 15 yr stand and approached zero in older stands (Fig. 2C). Kurtosis also was highest (1.90) in the 15 yr stand, but decreased to ca. -1 in the 25–29 yr stands and approached zero in the oldest stands.

The diameter distribution for the 15 yr stand was a significant, positively skewed function ($g_1 = 1.08$; $t = 4.41$, $p < 0.001$) (Fig. 3A). The distribution was also leptokurtotic (peaked) ($g_2 = 1.90$; $t = 3.88$, $p < 0.001$). The largest individual in this stand was ca. 10 cm in diameter. The 27 yr stand was not skewed, but was platykurtotic (flattened); however, neither value was statistically significant (Fig. 3B). The largest individual was ca. 37 cm in diameter or 3.7 times larger than the largest tree in the 15 yr stand. In the 33 yr stand, the distribution was slightly, positively skewed and was platykurtotic (Fig. 3C). No individuals were found in the smallest size classes. The largest individual was 26 cm in diameter. No *A. smallii* plants were found in the mature stands (>150 yr).

The number of stems per plant (both live and dead) for *A. smallii* was time dependent (Fig. 4). In the 15 yr stand, number of stems per plant ranged from 1–17 with no dead stems (Fig. 4A). In the 27
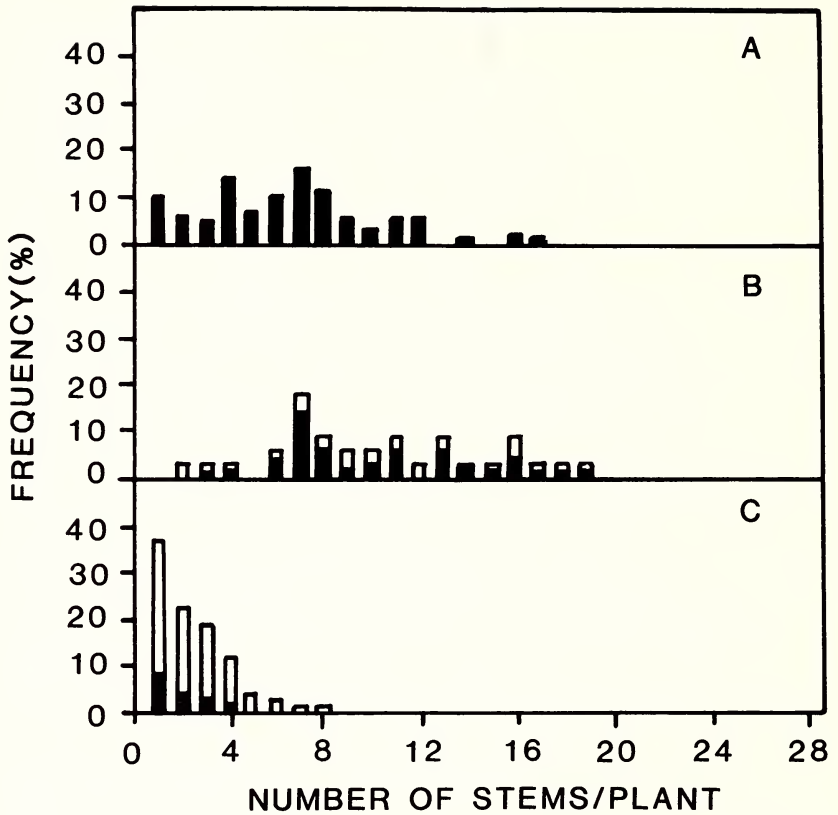
Fig. 4. Frequency distribution of number of stems/plant in a 15 yr stand (A), a 27 yr stand (B), and a 33 yr stand (C). ■ = live stems; □ = dead stems.

yr stand, number of stems per plant ranged from 2–18. There were no single stemmed plants and those standing with 2 stems were dead. In general, almost all other plants had 50% dead stems (Fig. 4B). In the 33 yr stand, number of stems was reduced to 1–8 per plant, more than 50% of the stems per plant were dead, and many of the larger trees were dead (Fig. 4C).

DISCUSSION

In many areas of southern Texas, *Acacia smallii* is a pioneer woody species that colonizes abandoned farmland or rangeland. Although it increases in density and basal area, community dominance of *A. smallii* only lasts approximately 30 yr, at which time it is replaced by mature community species (Van Auken and Bush 1985). Demographic characteristics examined showed the fate of *A. smallii* in

older stands. Density decreased and basal area increased, as has been shown for other early successional forest species (e.g., Spurr and Barnes 1973). Furthermore, a self-pruning of stems occurred; thus, the tendency of growth form was toward single stemmed trees in older communities. Finally, with overtopping by *Celtis laevigata* and subsequent additional shading, the remaining trees died.

Acacia smallii seems to follow the pattern of frequency distribution that was proposed by Mohler et al. (1978) for *Prunus pennsylvanica* L. In the present study, the 15 yr stand was well beyond their "establishment" and "transition" stages, but was similar to their "start of thinning" stage, which is a positively skewed function. Phytosociological data showed an increase in the basal area of *A. smallii* from the 15–27 yr stands, but a 46% decrease in density, which supports the start of thinning hypothesis. Although none of the frequency distributions in the present study were normal, the distribution in the late successional community did approach a normal curve similar to the "late thinning" stage.

The differences between the present study and the frequency distributions of single species proposed by Mohler et al. (1978) are probably due to several factors. In addition to intraspecific competition that causes thinning in plant populations, interspecific competition was probably also playing a critical role in shaping the frequency distribution of *A. smallii*. In the early stand, thinning was most likely through the death of the smallest individuals; however, in the mid- and late stands, death occurred to parts of whole plants before the individuals died. Whereas in the early stands none of the individuals had dead stems, the mid- and late stands showed increased death to stems of individuals. In addition, in the mid- and late stands, there was no recruitment of *A. smallii*.

Whittaker (1975) suggested that colonizing species would develop bell-shaped frequency distributions, whereas mature community species would have negative exponential distributions. This is probably an oversimplification, and dependent on episodic seedling establishment. Furthermore, his data suggested that, as the population of a colonizer ages, the distribution remained normal, but frequency of individuals in each size or age class would be reduced by deaths.

Changes in the available resources in a temporal sequence greatly affect the competitive ability of the species involved and, therefore, affect the frequency distributions. *Acacia smallii* is a heliophyte and tolerates low levels of soil nitrogen (Van Auken et al. 1985, Bush and Van Auken 1986a). Consequently, early in succession, *A. smallii* is a better competitor than late community species, which require higher levels of soil nitrogen (Van Auken et al. 1985, Bush and Van Auken 1986a). In early stands, therefore, intraspecific competition is probably more intense for *A. smallii* than interspecific competition; hence, smaller individuals often die. In older stands,

light becomes limiting and soil nitrogen levels favor the late com-
munity species (Bush and Van Auken 1986a,b). These conditions
apparently do not allow recruitment of *A. smallii* (Van Auken and
Bush 1985), whereas interspecific competition affects the larger in-
dividuals through the death of stems and, finally, the death of the
trees. In the mature forest, *A. smallii* disappears and species such
as *Celtis laevigata* dominate because they are better competitors in
the canopy shade.

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